

# Ocean-estuary coupling in the Oregon upwelling region: abundance and transport of juvenile fish and of crab megalopae

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**ABSTRACT:** Numerous species of fish and invertebrates move between the continental shelf and estuaries during their early life-history. The physical mechanisms that regulate such movement and the extent of coupling between the near-shore ocean and estuaries are poorly understood. It is unclear how, or whether, similar physical mechanisms regulate transport to the outer coast and between the outer coast and estuarine areas. We used high frequency light trap collections at 2 sites, outer coastal and estuarine, to compare the timing and magnitude of the relative abundance of juvenile fish and crab megalopae. The time series of juvenile fish and crab megalopae were statistically compared with physical variables indicative of wind and tidal conditions to identify potential transport mechanisms. Species examined included juvenile *Engraulis mordax* (northern anchovy), *Sardinops sagax* (Pacific sardine), *Sebastes melanops* and *S. caurinus* (black and copper rockfish), and megalopae of *Cancer magister* (Dungeness crab), *C. oregonensis* and *C. productus* combined (pygmy and red rock crabs), and *Pagurus* spp. (hermit crabs). The abundances of juvenile *E. mordax* and *S. sagax* and *C. magister* megalopae in the estuary were significantly cross-correlated with abundances at the outer coast (at 0 to –4 d lags). These data support the idea that estuarine ingress may be a 2-stage process with initial arrival in the near-shore as the first stage and subsequent entrance into nearby estuaries as the second stage. Significant cross correlations between species abundance and physical variables indicative of wind-driven transport, both upwelling and downwelling-related, and tidal transport, specifically the spring-neap tidal cycle, were found at both the outer coast and estuarine site. These data indicate that both wind-driven and tidal transport may contribute to the cross-shelf transport and estuarine ingress of organisms.

**KEY WORDS:** Ocean-estuary coupling · Juvenile fish · Crab megalopae · Upwelling region

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## INTRODUCTION

The exchange of materials, such as nutrients, plankton, and nekton, between estuaries and the ocean is of key interest to coastal scientists. Many species of fish and invertebrates move between the continental shelf and estuaries during their early life-history (Gunderson et al. 1990, Thorpe 1994, DiBacco et al. 2001, Epifanio & Garvine 2001). A common assumption in marine population ecology is that population size is altered by larval transport toward or away from adequate rearing or settlement areas which, for many species, are in coastal ar-

reas (Hjort 1914, Cushing 1975, Sinclair 1988). The regulation of population cycles may, in some cases, depend on how and when transport to and exchange between the coastal ocean and estuaries occurs.

The dominant mechanisms of cross-shelf transport and estuarine ingress include wind-driven Ekman transport, tidal stream transport through vertical migrations, non-linear internal waves and bores, moving frontal systems, and density-driven currents (Shanks 1983, 1988, Pineda 1991, Shanks et al. 2000, Epifanio & Garvine 2001, Forward & Tankersley 2001). Which of these mechanisms, if any, dominate transport to near-

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shore areas and ingress into estuaries is not well understood. It is also unclear how, or whether, similar physical mechanisms regulate transport to and between outer coast and estuarine areas. If estuarine ingress of coastal organisms is a 2 stage process, with the initial arrival in the near-shore as the first stage, and subsequent entrance into nearby estuaries as the second stage (Boehlert & Mundy 1988), each stage may be regulated by different transport mechanisms.

Estuaries worldwide are known to be nursery and/or settlement areas for numerous species of coastal fish and invertebrates (Elliott & Hemingway 2002). Some NE Pacific species, such as the northern anchovy *Engraulis mordax* and Dungeness crab *Cancer magister*, enter estuaries as larvae and juveniles. The potential advantages to estuarine residence include increased prey and refugia, which may increase growth and enhance survival (Miller & Dunn 1981, Gunderson et al. 1990, Jackson et al. 2001). However, the proportion of individuals within a cohort that enter estuaries, and the timing of and mechanisms regulating that entrance, are not well known.

In this study, simultaneous measurements of the abundance of juvenile fish and crab megalopae at an outer coastal and an estuarine site provide information on transport mechanisms and the exchange of organisms between the coastal ocean and an adjacent estuary. We collected organisms from late spring through early fall to compare the timing of arrival and relative abundance at each site. We also used these data to identify potential wind-driven and tidal-transport mechanisms. We chose an estuarine site within Coos Bay, Oregon, and a nearby outer coastal site to address these topics. Coos Bay is at the southern end of the Pacific Northwest region, defined as Vancouver Island, British Columbia to Cape Blanco, Oregon (Parrish et al. 1981). The area is characterized by seasonal, wind-driven upwelling (during late spring/summer) and downwelling (during late fall/winter) due to Ekman transport of surface waters (Huyer 1976).

During spring and summer in Oregon, northwesterly winds result in persistent upwelling and the establishment of an upwelling front where low density offshore waters meet high density, recently upwelled waters (Mooers 1976). The upwelling front is a convergence zone that can lead to increased concentrations of organisms (Peterson et al. 1979). Research efforts have focused on the role of upwelling relaxation and the shoreward movement of this front in promoting shoreward transport of larvae within the front (Roughgarden et al. 1988, Wing et al. 1995b, Shanks et al. 2000). We hypothesized that wind-driven transport, specifically associated with upwelling relaxation, would be a factor regulating the abundance of juvenile fish and crab megalopae at the outer coastal site.

Non-linear internal tides and bores and tidal stream transport through vertical migration may also cause shoreward transport of organisms. Internal tides are generated at the shelf break or over other topographic features on the seafloor and typically occur on diurnal and semi-diurnal frequencies (Kropfli et al. 1999, Inall et al. 2000). Although the mechanisms are not well understood, the generation and strength of internal tidal waves depend on the degree of water column stratification and their structure and frequency vary throughout the spring-neap tidal cycle. Strong spring tidal currents can generate more frequent and widespread internal tidal waves (Kropfli et al. 1999). Numerous studies document increased concentrations of larval fish and invertebrates (Shanks 1983, 1988, 1995, 1998, Shanks & Wright 1987, Pineda 1991, 1994), juvenile fish (Kingsford & Choat 1986), and small adult fish (Rogachev et al. 1996) in slicks associated with internal waves and bores. Some of these studies (Shanks 1983, 1988, Shanks & Wright 1987) directly observed the shoreward transport of material concentrated in slicks associated with internal waves and/or identified tidal frequencies in the near-shore abundance of larval invertebrates and fish (Shanks 1983, 1988, 1998, Pineda 1991, 1994, Johnson & Shanks 2002). Furthermore, modeling efforts demonstrate the potential for net horizontal transport to occur in organisms that undergo diel vertical migration in oscillatory tidal currents over the continental shelf (Hill 1998). If an organism was transported shoreward due to tidal stream transport, a tidal periodicity in near-shore abundance would also be expected, but the overall abundance pattern should be proportional to water flux and, therefore, to tidal range. We hypothesized that, at the outer coast, there would be a tidal periodicity in the abundance of species, which could be due to either of these tidally driven mechanisms.

The physical oceanography of Oregon's estuaries is strongly influenced by the coastal ocean (Roegner & Shanks 2001, Roegner et al. 2003). Therefore, we hypothesized that the estuarine abundance of post-larvae and juveniles of species that use estuaries as a nursery would be temporally correlated with their abundance at the outer coast. Furthermore, tidal stream transport can promote the ingress and retention of larvae and juveniles in estuaries (Forward & Tankersley 2001). Estuarine ingress may also be associated with on-shore or downwelling winds that force coastal waters into the estuary (Goodrich et al. 1989). Therefore, we predicted that both tidal and wind-driven transport would promote the estuarine ingress of juvenile fish and crab megalopae.

To examine these hypotheses, the time series of juvenile fish and crab megalopae abundances from the outer coast and estuarine sites were statistically com-

pared with each other and with physical variables indicative of wind and tidal conditions (e.g. sea surface temperature, along-shore and cross-shore wind stress, upwelling index, and daily tidal range). This allowed us to compare the timing and magnitude of the relative abundance of organisms at the 2 locations and identify potential transport mechanisms. Given the difficulty involved with tracking marine larvae, inferences regarding larval transport are often made through correlations between species abundance and physical variables (Shanks 1983, Johnson et al. 1986, Shanks & Wright 1987, Pineda 1991, Jones & Epifanio 1995, Wing et al. 1995b, Shanks 1998, Findlay & Allen 2002).

## MATERIALS AND METHODS

**Study area.** Samples were collected at 2 sites: Coos Bay and Sunset Bay. The Coos Bay estuary is located on Oregon's south coast (Fig. 1). The drowned river valley Coos Bay is, at approximately 54 km<sup>2</sup>, the second largest estuary in Oregon. Tides are mixed, semi-diurnal with a mean amplitude of 2.3 m. Sunset Bay is an outer coast embayment, approximately 2 km south of the entrance to Coos Bay. A small tributary, Big Creek, empties into Sunset Bay. During summer months, when

the majority of the data were collected, Big Creek monthly flow is minimal, <0.02 to 0.08 m<sup>3</sup> s<sup>-1</sup> mo<sup>-1</sup> (Coos County Water Resources Department data).

**Biological data.** Light traps were used to collect organisms. Traps consisted of a 10 l polycarbonate (clear) carboy with 10 circular funnel openings (1 to 1.25 cm in diameter) and an 8 W fluorescent light in a sealed tube powered either by shore power or with a 12.0 volt, 12.0 AH rechargeable Pb-Acid battery controlled with a photocell (Fig. 2). Three light traps were deployed at each of 2 sites: (1) within the South Slough, approximately 1 km inside of Coos Bay (43° 20' 12" N, 124° 19' 14" W) and (2) at Sunset Bay, approximately 2 km south of Coos Bay (43° 20' 7" N, 124° 22' 23" W) (Fig. 1). Traps within each site were deployed 15 to 30 m apart, from June 9 to October 12, 2000. Samples from Coos Bay were collected daily throughout the study whereas Sunset Bay samples were collected daily for the initial 31 d of the study and then collected every other day for the remaining 96 d. Sunset Bay will be referred to hereafter as the 'outer coast site' and Coos Bay as 'the estuarine site'. Juvenile fish and crab megalopae were identified to species or, in some cases, genus, and counted. Standard lengths (SL) of fish were measured to the nearest millimeter.

Light traps are passive collectors of positively phototactic organisms. Although collection is biased to organisms with positive phototaxis, light traps offer a

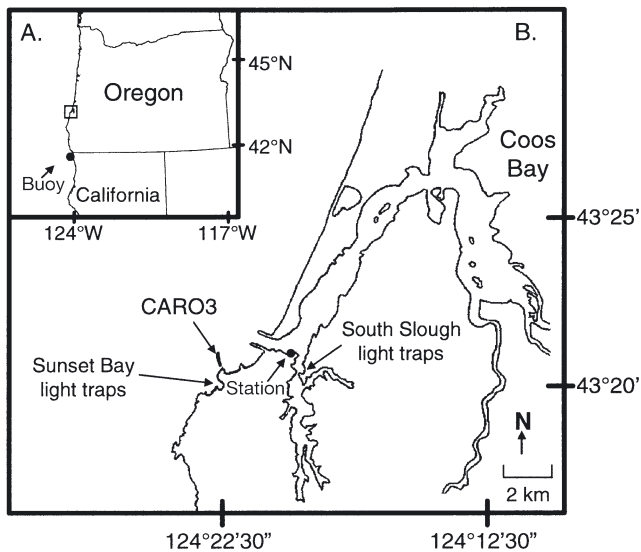


Fig. 1. Study sites in Oregon. (A) Region of study & location of NOAA Buoy #46027 (41° 51' 01" N, 124° 22' 52" W), which provided surface water temperature data (0.6 m water depth) for outer-coast analysis. (B) Location of Sunset Bay (outer coast site) and South Slough (estuarine site) light traps; and location of NOAA Stn #9432780 (43° 20' 42" N, 124° 19' 21" W), which provided surface water temperature data for estuarine analysis. NOAA's C-MAN Stn CAR03 (43° 20' 30" N, 124° 22' 30" W), which provided daily wind speed and direction, is labeled. Note 2 km scale bar

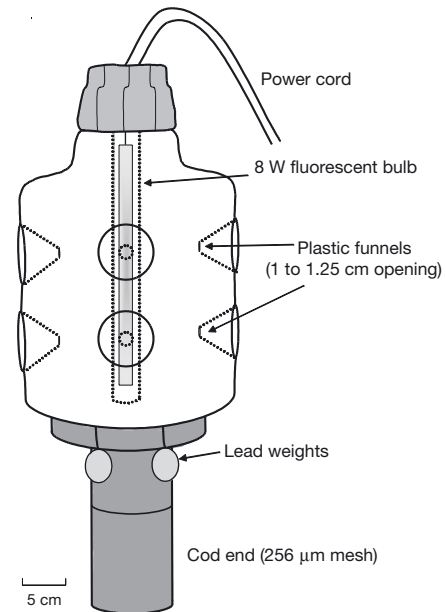


Fig. 2. Light traps used to collect organisms in outer coast and estuarine waters. Each trap had 10 funnel openings (1 to 1.25 cm in diameter) and an 8 W fluorescent light in a sealed tube powered either by shore power or with a 12.0 V, 12.0 AH rechargeable Pb-Acid battery controlled with a photocell. Note 5 cm scale bar

number of advantages to more traditional net collections which made them appropriate for this study. The use of light traps allows for simultaneous and integrated sampling over a relatively long period, i.e. the entire night. This increases the probability of capture of organisms found at low densities. Traps can be placed in near-shore coastal areas that are difficult to sample with more traditional, ship borne methods. Light traps often capture late-stage larvae and early juveniles, stages that are poorly sampled with nets (Milicich & Doherty 1994). Although there is only one published report of light traps being used in the North Pacific (Roegner et al. 2003), they have been used to collect larval and juvenile fish and invertebrates in tropical (Doherty 1987, Thorrold 1992, Kingsford & Battershill 1998) and temperate (Hickford & Schiel 1999) regions. Over 30 fish taxa (larvae and juveniles) and over 40 invertebrate taxa (larvae, juveniles, and adults) have been collected in light traps in Coos Bay (Miller & Shanks unpubl. data). In this study, we examined juvenile *Engraulis mordax* (northern anchovy), *Sardinops sagax* (Pacific sardine), *Sebastes melanops* and *S. caurinus* combined (black and copper rockfish), and megalopae of *Cancer magister* (Dungeness crab), *C. oregonensis* and *C. productus* combined (pygmy and red rock crabs), and *Pagurus* spp. (hermit crabs).

*Engraulis mordax* (northern anchovy) and *Sardinops sagax* (Pacific sardine) belong to the Families Engraulidae and Clupeidae, respectively. Both species produce pelagic eggs and larvae (Matarese et al. 1989). The northern extent of *E. mordax* is typically northern British Columbia, Canada. *S. sagax* extend farther north into southeast Alaska, USA. The southern extent of both species is southern Baja California, Mexico. *E. mordax* spawn throughout the year in California, but farther north spawning appears to be concentrated in summer months (Hart 1973). *S. sagax* spawn in central California from January to June, with a peak in April to May.

*Sebastes melanops* and *S. caurinus* (black and copper rockfish, respectively) belong to the Family Scorpaenidae, which are relatively long-lived, viviparous fishes with pelagic larval and juvenile periods typically between 2 and 5 mo. *S. melanops* range from southern California to the Aleutian Islands. *S. caurinus* range from Baja California to the Gulf of Alaska (Matarese et al. 1989). Juveniles of these 2 species are often found along the outer coast and in estuaries in late spring through summer.

*Cancer magister*, *C. oregonensis*, and *C. productus* undergo indirect development. A naupliar stage, typically passed within the egg, is followed by 5 zoeal and a megalopal (=post-larval) stage prior to metamorphoses to the benthic juvenile stage. In Oregon, females become ovigerous in the fall and release the first zoeal stage after a 3 to 4 mo brood period (Reilly

1983, Strathmann 1987). Settlement, which usually occurs along the coast or in estuaries, typically begins in April and peaks in May but can continue through the fall (Lough 1975, Gunderson et al. 1990, Roegner & Shanks unpubl. data). The entire larval period for *C. magister* (Dungeness crab) ranges between 75 and 180 d with the final 25 to 30 d as megalopae (Reilly 1983, Strathmann 1987, Moloney et al. 1994). The larval period of *C. oregonensis* (pygmy rock crab) is estimated at 155 d, with a range of 123 to 203 d (Lough 1975). Due to similarities in size and appearance, *C. oregonensis* and *C. productus* were indistinguishable as megalopae and were combined for all analyses.

The *Pagurus* spp. crabs also undergo indirect development. They pass through 4 zoeal stages and 1 megalopal stage prior to metamorphoses to a benthic juvenile. Larval durations are estimated to average 49 to 76 d with the final 17 to 19 d as megalopae (Strathmann 1987).

**Physical data.** Average daily wind speed and direction were calculated from hourly data obtained from the National Oceanic and Atmospheric Administration's (NOAA) National Data Buoy Center's C-MAN Stn CAR03 (43° 20' 30" N, 124° 22' 30" W), which is located on the outer coast between Sunset Bay and the mouth of Coos Bay (Fig. 1). In the vicinity of Coos Bay, the coastline of Oregon is oriented 20° northeast of true north. Therefore, wind direction was corrected for the angle of coast by subtracting 20° from the average daily wind direction. Daily average along-shore and cross-shore wind stress were calculated using the daily average wind speed and direction, a constant drag coefficient ( $C_D = 0.00122$ ) and air density ( $\rho_a = 0.0013$ ) (Pedolsky 1987). Because we used a constant drag coefficient, the reported wind stress should be considered pseudo-stress values. For the outer coast time series, hourly surface water (0.6 m depth) temperatures (°C) were obtained from offshore NOAA Buoy #46027 (41° 51' 01" N, 124° 22' 52" W), which was the closest working coastal buoy during this study (Fig. 1). For the estuarine time series analyses, hourly surface water temperatures (°C) were obtained from NOAA Stn #9432780 (43° 20' 42" N, 124° 19' 21" W), located near Coos Bay's south jetty. Maximum daily tidal range (cm) was obtained from Harbor Master™ software program. Upwelling indices (at 45° N, 125° W) were obtained from the NOAA Pacific Fisheries Environmental Laboratory (PFEL), Pacific Grove, California. PFEL coastal upwelling indices are calculated based upon Ekman's theory of mass transport due to wind stress. Ekman transports are resolved into components parallel and normal to the local coastline orientation. The magnitude of the offshore component is considered to be an index of the amount of water upwelled from the base of the Ekman layer. Positive values are, in general, the result of equator-ward wind stress.

Negative values imply downwelling, or the on-shore advection of surface waters accompanied by a downward displacement of water. The index is produced from 6-hourly fields of surface pressure on a global spherical  $1^\circ$  mesh (a  $180 \times 360^\circ$  grid). The standard west coast 6-hourly upwelling indices are a product of the  $3^\circ$  pressure field interpolated from the  $1^\circ$  grid. Units for upwelling indices are  $100 \text{ m}^3 \text{ s}^{-1}$  per meter of coastline. Daily averages were calculated for offshore and estuarine surface water temperature and the upwelling index.

**Statistical analysis.** Outer coast samples were initially collected daily and then every other day. Therefore, daily collections were summed over 2 d to ensure valid comparisons with collections made every other day, which resulted in 64 samples. The physical data series were averaged over 2 d periods for comparison with the outer coast biological data series. For the estuarine site, however, daily measurements of both biological and physical variables were used to determine potential transport mechanisms, which resulted in 127 samples. For all paired comparisons between biological data from the outer coast and the estuary, 2 d sums (64 samples) were used.

Species abundance data were log transformed to reduce the influence of large peaks in the series and examined for trends and/or auto-correlations (Emery & Thomson 1987). If biological data displayed a seasonal trend and/or significant auto-correlation, data were smoothed with an unweighted moving average (10 d average in the estuary and 4 d average at the outer coast) (Fig. 3A,B). The difference, or residual, between the data series and the smoothed data was then computed with Eq. (1):

$$X_t = Y_t - Z_t \quad (1)$$

where  $X_t$  is the residual at time  $t$ ,  $Y_t$  is the raw data at time  $t$ , and  $Z_t$  is the smoothed data at time  $t$  (Quinn & Keough 2002) (Fig. 3C). Residuals were then smoothed with a 2 sample moving average (i.e. 2 d in the estuary and 4 d at the outer coast) (Fig. 3D). If a physical data series had a seasonal trend, the trend was removed with Eq. (2):

$$X_{dt} = X_{it} - (a + b \times t) \quad (2)$$

where  $X_{dt}$  = detrended value at time  $t$ ,  $X_{it}$  = original value at time  $t$ ,  $a$  (intercept) and  $b$  (slope) are computed from the original data series via least squares regression, and  $t$  = time, e.g. sample day. Statistica™ time series analysis was used to calculate cross correlations between biological and physical series. Time series analysis is used to measure the strength of a relationship between 2 variables. In this study, lags between variables represent days; the sign indicates whether peaks in lagged series occurred after (nega-

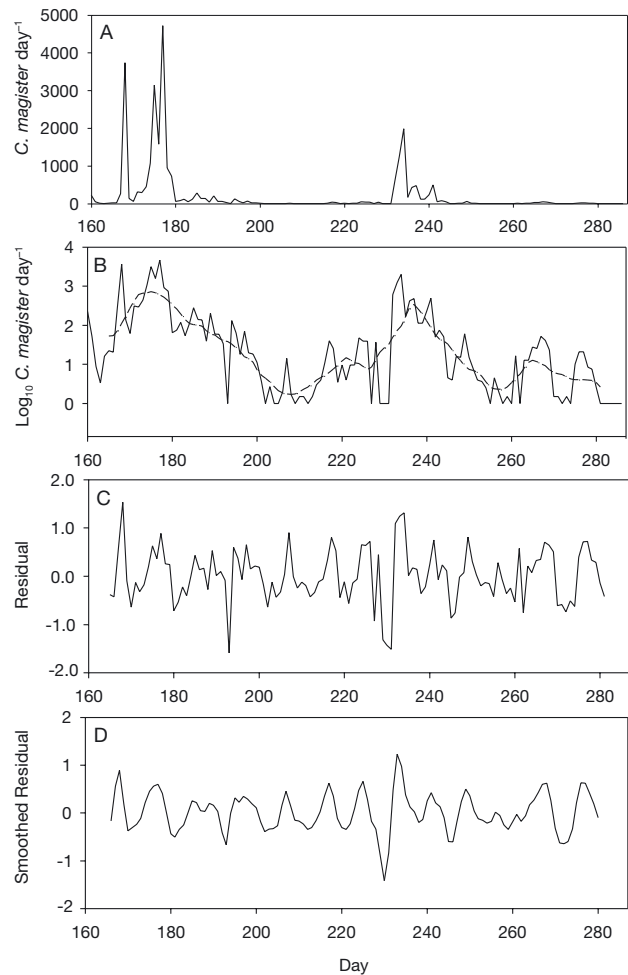


Fig. 3. *Cancer magister*. (A) Average abundance of Dungeness crab collected per day at the estuarine site. (B)  $\log_{10}$  average abundance (solid line) and 10 d moving average (dashed line). (C) Difference, or residual, between  $\log_{10}$  daily abundance and 10 d moving average. (D) Smoothed (2 d) residuals for data in (C)

tive values) or before (positive values) changes in the other variable. Positive (negative) cross-correlations indicate a positive (negative) relationship between variables. A significant statistical correlation does not necessarily imply a cause and effect relationship. Typically, in time series analyses, only lags  $<10\%$  of the length of the time series are considered valid. Therefore, only lags  $<6$  d at the outer coast and  $<12$  d at the estuarine site are presented (Emery & Thomson 1987).

Species abundances at the outer coast and estuarine site were compared in 2 ways: (1) the average catch of 3 light traps per location for each sample day (64 samples from each site) and (2) the average total catch of 3 light traps per location over the entire study (3 samples from each site). Species abundance at both sites was typically pulsed, with numerous days of low or no

catch. Few, even log-transformed, biological time series met the assumption of normality. Therefore, the average catch per sample for each species at the 2 sites ( $n = 64$ ) was compared with the non-parametric Mann-Whitney  $U$ -test. Similarly, for fish length (SL), only *Sardinops sagax* data were normally distributed. Therefore, for consistency and because statistical results did not differ between parametric and non-parametric approaches, average fish size (SL) per site was compared with the Mann-Whitney  $U$ -test. For sample sizes  $<20$ , the Mann-Whitney  $U$ -test  $U$  statistic for small samples is presented in lieu of the  $Z$  statistic (Sokal & Rohlf 1987).

## RESULTS

### Physical setting

The majority of the study occurred during the summer upwelling period when winds are predominantly northwesterly (Fig. 4A). Upwelling favorable winds occurred during 73% of the study while downwelling favorable winds occurred the remaining 27% (Fig. 4A,B). Water temperatures averaged  $10.8 \pm 1.4^\circ\text{C}$  ( $\pm\text{SD}$ ) with a range of  $7.0$  to  $14.2^\circ\text{C}$  along the outer coast and  $11.7 \pm 0.9^\circ\text{C}$  ( $\pm\text{SD}$ ) with a range of  $10.4$  to  $14.8^\circ\text{C}$  inside the estuary (Fig. 4C). Along-shore and cross-shore wind stress were strongly negatively correlated (0 d lag:  $r = -0.79$ ), i.e. when along-shore wind stress was positive (northward), cross-shore wind stress was typically negative (westward) (Fig. 4A). Water temperature at the outer coast buoy and estuarine station were significantly correlated with each other ( $-1$  d lag:  $r = +0.60$ ) and with along- and cross-shore wind stresses (0 to  $-2$  d lags:  $r \geq \pm 0.40$ ), i.e. positive along-shore and negative cross-shore wind stresses (downwelling winds) were correlated with warmer sea surface temperatures. Positive values of the upwelling index (at  $42^\circ\text{N}$   $125^\circ\text{W}$ ) were significantly correlated with negative (southward and upwelling favorable) along-shore wind stress (0 d lag:  $r = -0.66$ ). Positive cross-shore wind stress (eastward) was significantly positively correlated with the upwelling index (0 d lag:  $r = +0.48$ ). Therefore, surface water temperatures decreased and upwelling indices increased with winds from the northwest. The opposite conditions (i.e. winds from the south-southeast) resulted in warmer water temperatures and lower upwelling indices.

### Biological data

Eight species of fish and 8 species of invertebrates were collected from both the outer coast and estuarine

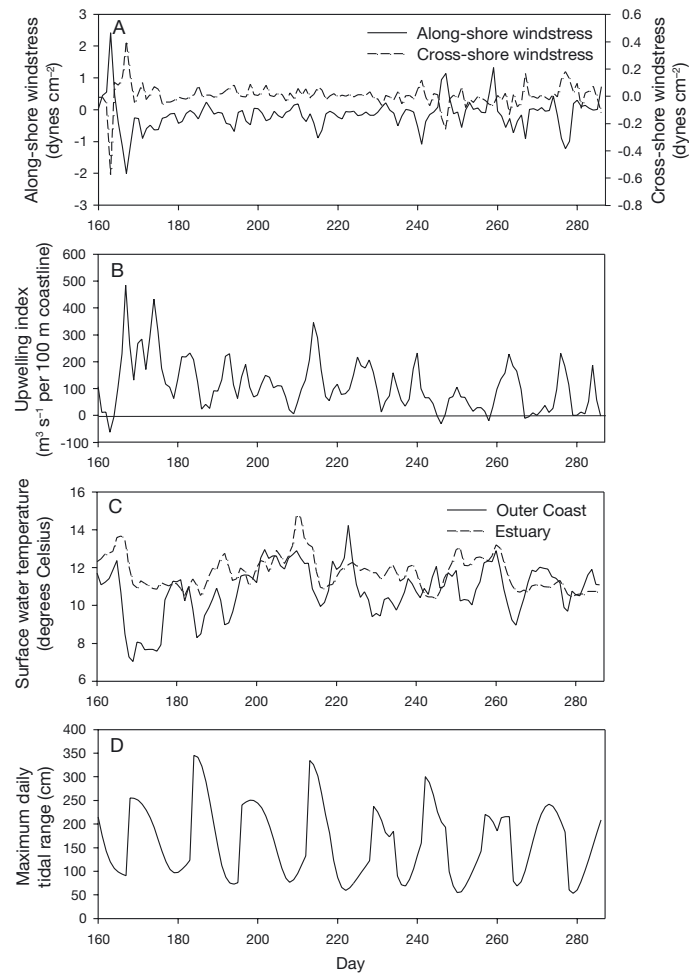


Fig. 4. Time series of the physical variables during the 127 d study. (A) Average daily along-shore and cross-shore wind stress ( $\text{dynes cm}^{-2}$ ). Positive values are northward (along-shore) and eastward (cross-shore); negative values are southward (along-shore) and westward (cross-shore). Data are from NOAA's C-MAN Stn CAR03 ( $43^\circ 20' 30'' \text{N}$ ,  $124^\circ 22' 30'' \text{W}$ ). (B) Average daily upwelling indices ( $\text{m}^3 \text{s}^{-1}$  per 100 m of coastline) at  $45^\circ \text{N}$ ,  $125^\circ \text{W}$ . Data are from NOAA's Pacific Fisheries Environmental Laboratory. (C) Average daily surface water (0.6 m depth) temperature ( $^\circ\text{C}$ ). Outer coast data are from NOAA Buoy #46027 ( $41^\circ 51' 01'' \text{N}$ ,  $124^\circ 22' 52'' \text{W}$ ) and estuarine data are from NOAA Stn #9432780 ( $43^\circ 20' 42'' \text{N}$ ,  $124^\circ 19' 21'' \text{W}$ ). (D) Maximum daily tidal range (cm). Data are from Harbor-Master™ tidal prediction program

site (Table 1). Average correlations of catch between light traps within a site during the study were  $r^2 = 0.50$  for *Engraulis mordax* and  $r^2 = 0.80$  for *Cancer magister*. The lower correlation for *E. mordax* is due, in part, to their lower total catch ( $<500$  individuals) compared with the total catch ( $>20\,000$  individuals) of *C. magister*. Abundances at the 2 sites were compared if a species or genus was present in light traps  $>5\%$  of the time, which included juvenile *Engraulis mordax*

Table 1. Juvenile fish and crab megalopae collected in light traps at both the outer coast and estuarine site. Size range (standard length; SL) for fishes is included. Species in **bold** are discussed in the text

Taxon	Common name	Size (mm) or Stage
Fishes		
<b><i>Engraulis mordax</i></b>	Northern anchovy	21–80
<b><i>Sardinops sagax</i></b>	Pacific sardine	35–71
<b><i>Sebastes melanops</i></b>	Black rockfish	20–61
<b><i>Sebastes caurinus</i></b>	Copper rockfish	20–33
<i>Gobiosox maeandricus</i>	Clingfish	7–11
<i>Scorpaenichthys marmoratus</i>	Cabezon	30–47
<i>Clinocottus globiceps</i>	Mosshead sculpin	12–16
<i>Arctedius</i> sp.	Sculpin	14–18
Crabs		
<b><i>Cancer magister</i></b>	Dungeness crab	Megalopae
<b><i>Cancer oregonensis/productus</i></b>	Pygmy/red rock crab	Megalopae
<i>Hemigrapsus oregonensis</i>	Yellow shore crab	Megalopae
<b><i>Pagurus</i> spp. A and B</b>	Hermit crab	Megalopae
<i>Pachycheles</i> sp.	Porcelain crab	Megalopae
<i>Petrolisthes</i> sp.	Porcelain crab	Megalopae

### Northern anchovy *Engraulis mordax*

The abundances of juvenile *Engraulis mordax* at the outer coast and estuarine sites were significantly cross-correlated. Peaks in estuarine abundance tended to occur 2 to 4 d after peaks in outer coast abundance ( $r = +0.36, +0.40$ , respectively,  $p \leq 0.05$ ) (Fig. 5A). More *E. mordax* were collected at the outer coast compared to the estuarine site although the difference was not statistically significant (Table 2). The average size (SL) of outer coast individuals was significantly larger than those collected in the estuary (Table 3).

A tidal signal was evident in the abundance of *Engraulis mordax* at both sites. Significant cross correlations between maximum tidal range and abundance occurred 0 to 2 d after

(northern anchovy), *Sardinops sagax* (Pacific sardine), *Sebastes melanops* and *S. caurinus* combined (black and copper rockfish), and megalopae of *C. magister* (Dungeness crab), *C. oregonensis* and *C. productus* combined (pygmy and red rock crabs), and *Pagurus* spp. (hermit crabs) (Table 2). Time series analyses were completed on all taxa present >25% of the time, which excluded *S. sagax* and the *Sebastes* species (Table 2). Sampling began after the initial seasonal pulse in *C. magister* settlement that typically occurs during May. However, data from estuarine light traps maintained year-round indicate that approximately 60% of the *C. magister* settlement in 2000 occurred during this study (Miller & Shanks unpubl. data).

spring tides at the outer coast (i.e. 0 to 2 d after spring tides and 4 d before neap tides) and between spring and neap tides in the estuary (i.e. 3 to 4 d after spring tides and 2 to 3 d before neap tides) (Table 4). Abundance at the outer coast was not cross-correlated with any other physical variables. Abundance in the estuary, however, was significantly cross-correlated with negative along-shore wind stress (upwelling favorable) and positive upwelling indices. These data suggest that there is a tidal periodicity in the transport of juvenile *E. mordax* to both the outer coast and the estuary, and that estuarine ingress may have occurred shortly after initiation of upwelling conditions.

Table 2. Abundance of juvenile fish and crab megalopae collected at the outer coast and estuarine sites. Percentage of days (% time) during the study that taxa were present in light trap samples is also presented. Abundance data are presented as (1) total mean abundance ( $\pm$ SE) over the entire study (average of 3 traps from each site,  $n = 3$ ) and (2) mean ( $\pm$ SE) per sample period (average of 3 light traps from each 2 d sampling period,  $n = 64$ ). Results from Mann Whitney *U*-test (*Z* statistic and *p*-value) for the mean per sample ( $n = 64$ ) are included

Taxon	% time	Total mean abundance ( $n = 3$ )		Mean per sample ( $n = 64$ )		Mann-Whitney	
		Outer Coast	Estuary	Outer Coast	Estuary	<i>Z</i>	<i>p</i>
<i>Engraulis mordax</i>	84.4	424.5 $\pm$ 12.7	182.0 $\pm$ 9.3	9.5 $\pm$ 3.8	2.8 $\pm$ 0.5	-1.3	0.18
<i>Sardinops sagax</i>	7.8	7.0 $\pm$ 3.3	5.7 $\pm$ 3.0	0.13 $\pm$ 0.09	0.02 $\pm$ 0.01	-0.8	0.43
<i>Sebastes melanops</i> / <i>S. caurinus</i>	20.3	5.0 $\pm$ 0.8	9.5 $\pm$ 2.1	0.09 $\pm$ 0.03	0.30 $\pm$ 0.21	-1.1	0.29
<i>Cancer magister</i>	98.4	513.5 $\pm$ 69.9	24928 $\pm$ 733.1	8.5 $\pm$ 1.8	404.3 $\pm$ 137.7	-5.8	<0.001
<i>Cancer oregonensis</i> / <i>C. productus</i>	50.0	77.5 $\pm$ 3.7	47.3 $\pm$ 12.2	2.3 $\pm$ 0.8	2.2 $\pm$ 1.8	0.9	0.36
<i>Pagurus</i> spp. A and B	29.7	678.0 $\pm$ 4.2	1.3 $\pm$ 0.30	23.1 $\pm$ 11.3	0.03 $\pm$ 0.02	-2.7	0.02

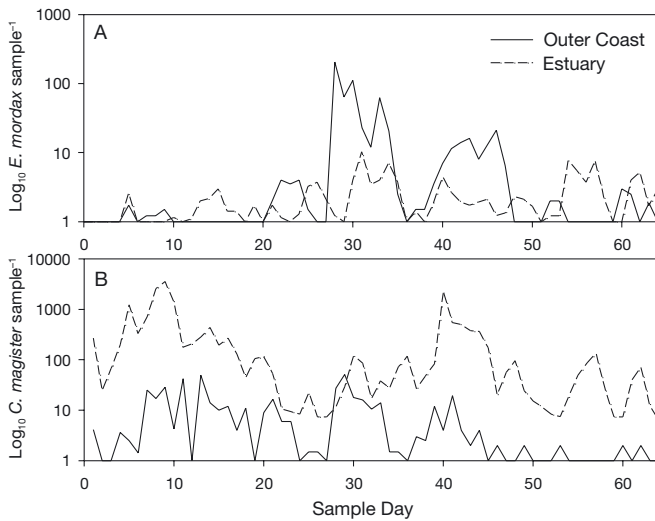


Fig. 5. *Engraulis mordax* and *Cancer magister*. Log-transformed abundance of (A) *E. mordax* and (B) *C. magister* collected per sample day ( $n = 64$ ) during the 127 d study. Daily collections were summed over 2 d periods for comparison with samples collected every other day

#### Pacific sardine *Sardinops sagax*

The abundances of juvenile *Sardinops sagax* at the outer coast and estuarine site were significantly cross-correlated, with peaks in estuarine abundance 0 and 2 d after peaks in outer coast abundance ( $r = +0.66$  and  $+0.90$ , respectively,  $p \leq 0.05$ ). More individuals were collected at the outer coast compared to the estuary, but the difference was not statistically significant (Table 2). The average size (SL) of individuals at the outer coast was significantly smaller than those in the estuary (Table 3). No further time series analysis was completed because *S. sagax* were present in the light traps for <25% of the study period (Table 2).

#### Pacific rockfish *Sebastes melanops* and *S. caurinus*

The abundance of juvenile *Sebastes* at the estuarine site was not correlated with abundance at the outer

coast. More individuals were collected at the estuarine site compared to the outer coast but the difference was not statistically significant (Table 2). The average size (SL) of individuals collected at the outer coast was not significantly different from those in the estuary (Table 3). *Sebastes* juveniles were present in light traps for <25% of the study period, therefore no further time series analysis was attempted (Table 2).

#### Dungeness crab *Cancer magister*

The abundances of *Cancer magister* megalopae at the outer coast and estuarine site were significantly cross-correlated. Peaks in estuarine abundance occurred 0 and 2 d after peaks in outer coast abundance ( $r = +0.39$  and  $+0.42$ , respectively,  $p \leq 0.05$ ) (Fig. 5B). However, significantly fewer *C. magister* were collected per sample at the outer coast ( $8.5 \pm 1.8$  SE) compared to the estuary ( $404.3 \pm 137.7$  SE) (Table 2).

*Cancer magister* abundances at the outer coast and in the estuary were significantly cross-correlated with the tides (Table 4). Significant cross correlations between maximum tidal range and abundance occurred 0 to 2 d after spring tides at the outer coast and, in the estuary, between spring and neap tides. The abundance of *C. magister* megalopae at both the outer coast and estuarine site were significantly cross-correlated with lower water temperatures, negative along-shore wind stress (southward and upwelling favorable), and positive upwelling indices (Table 4). These data suggest that *C. magister* megalopae may be transported shoreward during active upwelling, spring tides, or both, and estuarine ingress can occur during upwelling events and/or between spring and neap tides.

#### Pygmy and red rock crabs *Cancer oregonensis* and *C. productus*

The abundance of *Cancer oregonensis* and *C. productus* megalopae at the outer coast was not cross-correlated with abundance at the estuarine site. More individuals

Table 3. Mean standard length ( $\pm$ SD) and size range (mm) of juvenile fish collected at the outer coast and estuarine sites.  $n$  = number of fish used in analysis. Results of Mann-Whitney  $U$ -test ( $Z$  statistic and  $p$ -value) are included. For comparisons with <20 individuals, the  $U$  statistic is presented

Taxon	Outer Coast			Estuary			Mann-Whitney	
	Mean size (mm)	Range (mm)	$n$	Mean size (mm)	Range (mm)	$n$	$U$ ( $Z$ )	$p$
<i>Engraulis mordax</i>	$57.2 \pm 16.8$	28–80	712	$38.8 \pm 14.3$	21–71	269	13.1	<0.001
<i>Sardinops sagax</i>	$50.9 \pm 6.9$	35–61	14	$60.1 \pm 7.3$	41–71	16	31.5	<0.001
<i>Sebastes</i> spp.	$37.5 \pm 19.0$	20–61	8	$24.8 \pm 5.2$	20–60	18	59	0.46



Table 4. Time-series analyses between biological and physical variables at the outer coast and estuarine sites. Lags represent days; the sign indicates whether peaks in the biological series occur after (negative values) or before (positive values) changes in the physical variable. Cross-correlations are presented as positive (indicates a positive relationship between biological and physical variable) or negative (indicates a negative relationship) values. Positive along-shore wind stress cross-correlations indicate a relationship with northward winds; negative indicate southward winds. Positive cross-shore wind stress cross-correlations indicate eastward and negative indicate westward winds. Positive maximum tidal range cross-correlations indicate a relationship with spring tides; negative indicate neap tides. Only statistically significant ( $p \leq 0.05$ ) cross-correlations are presented. ns: no statistical significance; -: insufficient data for analysis

	Temperature	Along-shore wind stress	Cross-shore wind stress	Upwelling index	Max. tidal range
<b>Northern anchovy <i>Engraulis mordax</i></b>					
Outer coast	ns	ns	ns	ns	+0 d = +0.272 +4 d = -0.369 -2 d = +0.266
Estuary	ns	+0 d = -0.251 -1 d = -0.235	ns	-2 d = +0.248	+2 d = -0.387 +3 d = -0.426 -3 d = +0.279 -4 d = +0.410
<b>Dungeness crab <i>Cancer magister</i></b>					
Outer coast	+0 d = -0.265	+0 d = -0.261	ns	-2 d = +0.352	+0 d = +0.265 +4 d = -0.309 -2 d = +0.302
Estuary	+0 d = -0.333 -1 d = -0.302	+0 d = -0.235 -1 d = -0.220	ns	-2 d = +0.256 -3 d = +0.263	+1 d = -0.285 +2 d = -0.317 -4 d = +0.246 -5 d = +0.299
<b>Cancer crab <i>Cancer oregonensis</i> and <i>C. productus</i></b>					
Outer coast	-4 d = -0.318	ns	ns	ns	+4 d = -0.289 -4 d = +0.297
Estuary	+0 d = +0.229 -1 d = +0.238	-4 d = +0.204	-4 d = -0.206	ns	ns
<b>Hermit crab <i>Pagurus</i> spp. A and B</b>					
Outer coast	ns	+0 d = +0.320	ns	-2 d = -0.257	ns
Estuary	-	-	-	-	-

were collected at the outer coast site compared to the estuary but the difference was not statistically significant (Table 2).

The abundance of *Cancer oregonensis* and *C. productus* megalopae at the outer coast site displayed a tidal periodicity; significant cross correlations occurred between spring and neap tides (Table 4). Abundance at the outer coast site was also significantly cross-correlated with cooler water temperatures. No tidal signal was evident at the estuarine site. Abundance in the estuary, however, was significantly cross-correlated with warmer water temperatures and, although weakly, southeasterly wind stress (downwelling favorable) (Table 4). These data suggest that shoreward transport of post-larval *C. oregonensis* and *C. productus* may occur during upwelling and that downwelling conditions may promote estuarine ingress.

#### Hermit crabs *Pagurus* spp.

The total catch of *Pagurus* spp. megalopae at the outer coast site was 1489 individuals with an average

sample abundance of  $23.1 \pm 11.3$  SE individuals (Table 2). Few *Pagurus* spp. megalopae (<5 total) were collected in the estuary. Therefore, no further statistical analyses were completed on the estuarine time series. *Pagurus* spp. abundance at the outer coast was significantly cross-correlated with positive along-shore wind stress and negative upwelling indices (Table 4), suggesting that *Pagurus* spp. megalopae returned to the outer coast site after an upwelling relaxation or downwelling event.

## DISCUSSION

### Relative abundance

The data presented here provide evidence for temporal coupling between arrival at the outer coast and estuarine ingress for juvenile *Engraulis mordax* and *Sardinops sagax*, and *Cancer magister* megalopae. For these species, abundance in the estuary consistently peaked at the same time or shortly after (0 to -4 d lag) abundance at the outer coast. There were not enough

*Pagurus* spp. megalopae collected in the estuary to draw any conclusions regarding the relationship between shoreward transport and estuarine ingress.

For most taxa, the total abundance at the outer coast was greater or not different than that in the estuary. *Cancer magister* megalopae were the exception. In this case, estuarine collections were exceptionally large, >4 times larger than outer-coast collections. This remarkable difference may indicate a preferential use of estuaries by this species.

Extensive research on estuarine use by late-stage larval and juvenile *Cancer magister* has been carried out in Washington (Stevens & Armstrong 1984, McConnaughey et al. 1992, Eggleston et al. 1998). Only one study, however, directly compared abundance at the outer coast and in the estuary (Gunderson et al. 1990). Population estimates of *C. magister* juveniles, based on 5 yr of trawl surveys from the Washington coast and 2 adjacent estuaries, were highly variable. There were typically more 0+ juveniles (i.e. those <1 yr old) along the outer coast than in the estuaries and more 1+ juveniles (i.e. those >1 yr old) within the estuary than along the outer coast (Gunderson et al. 1990). It is difficult to make further comparisons between their study, which used bi-monthly beam trawls to collect juveniles, and ours, which used light trap collections of megalopae.

The other notable difference in species composition is that the average size of *Engraulis mordax* in the estuary (38.8 mm SL) was significantly smaller than at the outer coast (57.2 mm SL) (Table 3). Given that the size range of individuals in the estuary (21 to 71 mm) was similar to the size range at the outer coast (28 to 80 mm), size-dependent estuarine immigration may have occurred (i.e. proportionally more smaller individuals entered the estuary). This fits an observed pattern of size-dependent depth distribution in certain species where smaller fish are found in, and presumably moved to, shallower waters (Deegan 1990, Beck et al. 2001). Alternatively, larger individuals may have migrated back out of the estuary. The size range of *Sardinops sagax*, however, was also similar at both sites but the average size in the estuary ( $60.1 \pm 7.3$  mm SL) was greater than at the outer coast ( $50.9 \pm 6.9$  mm SL) (Table 3). The significantly larger average size of *S. sagax* in the estuary is contrary to such a model and is less easily explained, as an average of nearly 10 mm of growth is unlikely to occur in 2 d.

One concern with the light trap deployment in this study is that the outer coast traps were tethered to buoys whereas the estuarine traps were attached to floating docks. Fishes and invertebrates at all life-history stages have been shown to congregate around docks, pilings, and other floating objects (Hunter 1967, Kingsford 1999). Although we cannot rule out a possible dock effect in our study, we note that if it did occur,

then it occurred only in *Cancer magister*, as all other species were collected in similar or greater numbers at the outer-coast site. We know of no reason why such an effect would occur preferentially in *C. magister*.

## Transport mechanisms

### Tidal transport

Evidence for transport driven by the tides was found in all taxa except *Pagurus* spp. For both *Engraulis mordax* and *Cancer magister*, abundance at the outer coast tended to peak around spring tides while abundance in the estuary peaked between spring and neap tides. The outer coast abundance of *C. oregonensis* and *C. productus* megalopae peaked between spring and neap tides and no tidal signal was evident in the estuary. What can explain these patterns? Modeling efforts have shown that net horizontal displacement of zooplankton may occur in the presence of oscillatory tidal currents and daily vertical migrations (Hill 1998). However, if shoreward transport occurred solely due to tidal stream transport, abundance patterns would more likely be proportional to water flux, and therefore tidal range. We did not see evidence of this in our data (e.g. Fig. 3A). Rather, we saw relatively large, discrete peaks in abundance, which suggests that shoreward transport in these species was probably not promoted solely by tidal stream transport. Another potential mechanism of shoreward transport, possibly in conjunction with tidal stream transport, is non-linear internal tides and bores. Increased concentrations of larval fish and invertebrates (Shanks 1983, 1988, 1995, 1998, Shanks & Wright 1987, Pineda 1991, 1994), juvenile fish (Kingsford & Choat 1986), and small adult fish (Rogachev et al. 1996) have been observed in slicks associated with internal waves and bores. Tidal frequencies have also been identified in the near-shore abundance of larval invertebrates and fish observed in surface slicks associated with internal waves (Shanks 1983, 1998, Shanks & Wright 1987). Therefore, it is possible that enhanced shoreward transport of organisms via internal waves and bores, in combination with tidal stream transport, could have generated the abundance patterns that we observed.

### Wind-driven transport

We present evidence for wind-driven transport in *Engraulis mordax*, *Cancer magister*, *C. oregonensis*, *C. productus*, and *Pagurus* spp. Peaks in species abundance occurred during upwelling-favorable winds, during downwelling-favorable winds, or with no relation to pre-

vailing wind stress. The abundance of *C. magister* megalopae was significantly cross-correlated with upwelling favorable winds, colder water, and positive upwelling indices at both the outer coast and estuarine sites. For *C. oregonensis* and *C. productus* megalopae, abundance at the outer coast was significantly cross-correlated with colder water temperatures. Juvenile *E. mordax* abundance in the estuary was also related to indicators of upwelling, including upwelling favorable winds and positive upwelling indices. The only evidence for transport to the outer coast during downwelling was found in the *Pagurus* spp., whose outer-coast abundance was significantly cross-correlated with northward along-shore wind stress and negative upwelling indices. In the estuary, post-larval *C. oregonensis* and *C. productus* showed some, although weak, relationships with indicators of downwelling. Overall, these data indicate that shoreward transport and estuarine ingress may occur during both upwelling and downwelling. However, we found more evidence for transport during periods of upwelling rather than downwelling conditions.

The cyclic nature and commercial value of *Cancer magister* populations have resulted in a considerable amount of research on their settlement and recruitment (Peterson 1973, Hatfield 1983, Johnson et al. 1986, Wing et al. 1995a,b, Johnson & Shanks 2002, Roegner et al. 2003). Numerous attempts to relate physical conditions during various life-history stages to adult harvest have yielded equivocal results. Cross correlations between adult harvest and upwelling winds were found at a variety of lags, from 6 mo to 5 yr (Peterson 1973, Johnson et al. 1986, McConnaughey et al. 1992, Wing et al. 1995a,b). Johnson et al. (1986), for example, found significant correlations between upwelling favorable wind stress and adult harvest at lags of 4 and 5 yr along northern California, Oregon, and Washington. The authors note that the observation may result from 'on-shore transport during the late larval phase', although 'the exact mechanisms are unknown.' Our data suggest that the shoreward transport of post-larval *C. magister* and *C. oregonensis* and *C. productus* can occur during active upwelling.

How might shoreward transport be promoted during a period of predominantly offshore surface transport? Huyer (1976) found that during upwelling favorable winds on the Oregon coast, offshore flow occurred in a shallow surface layer less than 20 m thick. On-shore flow was strongest immediately below that surface layer and decreased with depth in the lower portion of the water column. Furthermore, the direction of movement of the very near-surface waters (upper centimeters) is typically less than the 45° shift from the prevailing wind direction predicted by Ekman theory and can be much closer to the actual wind direction (Brown et al. 1989). Thus, the northwesterly winds that

generate upwelling could push very near-surface waters and associated neustonic organisms shoreward and can result in the shoreward movement of water below the Ekman layer. Shoreward transport could occur during upwelling if organisms were below the surface layer or in the neuston.

The abundance of post-larval *Cancer oregonensis* and *C. productus* in the estuary and *Pagurus* spp. at the outer coast were significantly cross-correlated with indicators of downwelling. The shoreward transport of *Pagurus* spp. may be related to relaxation of the upwelling front and associated shoreward movement of water (Roughgarden et al. 1988, Shanks et al. 2000). The estuarine ingress of *C. oregonensis* and *C. productus* may be related to downwelling winds forcing surface waters into the estuary after individuals entered near-shore waters (Johnson & Shanks 2002).

We found tidal periodicities and evidence for wind driven transport, both upwelling- and downwelling-related, in the abundance of juvenile fish and crab megalopae at the outer coast and estuarine sites. It has been proposed that, in upwelling regions, species with pelagic larvae and relatively long dispersal periods should reproduce primarily during the downwelling season to avoid advection offshore due to upwelling generated Ekman transport (Parrish et al. 1981). Numerous species, including those in this study, have larvae in coastal waters during the upwelling season, i.e. from late April/May through September off the Oregon coast. There has been an emphasis on the importance of upwelling relaxations, which allow waters associated with the upwelling front to move towards shore, in returning individuals to shore (Roughgarden et al. 1988, Wing et al. 1995a,b, Shanks et al. 2000). We suggest, and our data support, that successful shoreward transport can also occur during periods of active upwelling. Organisms, depending on their depth distribution, may be transported on- or offshore during active upwelling. Emphasis on only one mechanism may be insufficient to consistently explain shoreward transport and successful settlement.

The delivery of material to the coast and its exchange between outer coastal and estuarine areas are key components of coastal, estuarine, and population ecology. Mechanisms of larval transport are under investigation due to their importance in the determination of population size and structure. This study, which is one of the first to simultaneously document post-larval crab and juvenile fish abundance at an outer coastal and adjacent estuarine site, identified strong coherence in the peak abundance of *Engraulis mordax*, *Sardinops sagax*, and *Cancer magister* at the 2 sites. We also found evidence for tidal and wind-driven transport at both locations. These data support the idea that estuarine ingress is a 2-stage process, and

indicate that both wind-driven and tidal transport mechanisms contributed to the shoreward transport and estuarine ingress of post-larvae and juveniles. Further investigation on individual behaviors, including depth distribution and vertical migrations, is needed to determine more specifically how such behaviors interact with physical processes to regulate shoreward transport and estuarine ingress.

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